On the Blood-Vascular System of the Earthworm Pheretima, and the Course of the Circulation in Earthworms.

By

Karm Narayan Bahl, D.Sc.,

Of the Muir Central College, Allahabad, India.
(From the Department of Comparative Anatomy, Oxford.)

With 11 Text-figures.

Table of Contents.

I. Introductory.

The blood-vascular system of earthworms has engaged the attention of many distinguished observers. Lankester (**12**) described the blood-vessels of Lumbricus in one of his memoirs on the 'Anatomy of the Earthworm', which forms about the earliest contribution to this subject. Jaquet (**9**) gives a comparative account of the vascular system in Annelids, describing the system in typical genera of the various classes of the group. Of the Oligochaeta, he selects Lumbricus as a type. Perrier (**13**) and Benham (**5**), also working on Lumbricus, describe the course of flow in all the blood-vessels from a study of the disposition of the valves; to Benham we also owe our knowledge of the blood-supply of the nephridium in Lumbricus (**6**). Harrington (**8**) gives a detailed account of the anatomy of the blood-system in Lumbricus with elaborate diagrams, and was the first to describe the arrangement of blood-vessels in the integument. Recently, Johnstone and his student, Miss Johnson (**10** and **11**), have published two papers on the course of blood-flow in Lumbricus demonstrating the course in various vessels by a series of interesting experiments and observations. The blood-system has thus been thoroughly studied in Lumbricus since that is the form studied as a type in Europe and America. Amongst the Oriental forms of Oligochaeta, Bourne (**1**) has described the blood-system in some detail in the Perichaete worm Megascolex and also in Moniligaster grandis (**2**, 1894), a huge worm about two feet long placed by Beddard in the group Microdrili. Besides Bourne's work on Megascolex, very little attention has been paid to the blood-system of the Perichaetidae, the largest family of earthworms.

The earthworm Pheretima (the genus Perichaeta sensu stricto) is now studied as a type of the Oligochaeta in Northern India and also at the Universities of Bombay and Calcutta, and it has become necessary, therefore, to have as complete a knowledge as possible of the anatomy of this form. An attempt has been made in this paper to present an account

of the blood-system of Pheretima and the course of blood-flow about which, even in Lumbricus, there has been a great divergence of opinion amongst the various observers. Some of the observations were made in India, but in this country, besides having an opportunity of examining the two English genera Lumbricus and Allolobophora, I was able to complete my work on Pheretima, having been lucky to obtain specimens of this Oriental form in the Lily-house of Kew Gardens.

The work was carried out in the Department of Comparative Anatomy at Oxford. I am indebted to Professor E. S. Goodrich for his keen interest in my work; he has made valuable suggestions, and has also found time to read through and correct the manuscript of the paper.

Although essentially the blood-systems of both Lumbricus and Pheretima can be reduced to a common type, there are important differences in the system in the two genera, which I have indicated in the text. Pheretima resembles Allolobophora rather than Lumbricus so far as the blood-system in the general body-region is concerned, while the system differs in important respects from that of Megascolex. As regards the course of the blood-flow studied by holding the vessels with fine forceps, by cutting the vessels and observing the direction of blood-flow, and by a study of the valves, I am led to confirm the observations and conclusions of Johnstone (**10** and **11**) and to reject part of Bourne's theory of the course of the circulation (**1**).

The typical arrangement of the blood-system in Pheretima is found behind the fourteenth segment, being metamerically repeated behind that segment. In the first fourteen segments, on the other hand, this typical arrangement is considerably modified, this modification, together with that shown in the digestive, reproductive, and nervous systems, being spoken of as cephalization. It will be convenient, therefore, to describe, as Harrington (**8**) does in the case of Lumbricus, first, the typical arrangement as it occurs in the region of the body of the worm behind the fourteenth segment, and then the

blood-vessels in the first fourteen cephalized segments, and finally to discuss the course of the circulation in the system.

2. The Typical Arrangement of the Blood-system in the Intestinal Region of the Body behind the Fourteenth Segment.

The blood-system in this system in this region of the body consists of (*a*) three longitudinal trunks running parallel to one another, namely, the dorsal, the ventral, and the subneural vessels; (*b*) the intestinal blood-plexus, situated in the wall of the gut, is directly connected with the dorsal and ventral vessels, and indirectly with the subneural; and (*c*) the commissural, integumentary, and nephridial vessels.

(*a*) The Longitudinal Trunks.

1. The dorsal vessel.—The dorsal vessel is the most prominent of all the blood-vessels in the worm and is rhythmically contractile. It runs along the mid-dorsal line immediately beneath the body-wall, between the latter and the intestine, and is at once seen lying on the gut, when the worm is opened by a mid-dorsal incision. In Lumbricus the dorsal vessel is heavily covered over with 'yellow cells', which must be removed before the vessel is seen; but in Pheretima the 'yellow cells' do not cover the dorsal vessel, so that the latter is at once prominent on dissection. Although lying close upon the gut, the dorsal vessel is not actually attached to the wall of the former in any portion of its course. It is single throughout its length and has thick muscular walls which are responsible for its contractility. The average diameter of this vessel is about 220 μ; it is narrowest at places where it pierces the intersegmental septa. On opening a narcotized worm, we can easily see the wave of contraction in this vessel travelling from behind forwards and consequently driving the blood in that direction. During its course through the body, the dorsal vessel, on piercing each septum, has a pair of forwardly-directed valves (figs. 7 and 10) in its lumen. These valves,

as I shall show later, prevent the flow of blood backwards when the vessel contracts. There are also valves (vide infra) at the orifices of the dorso-intestinal and commissural vessels.

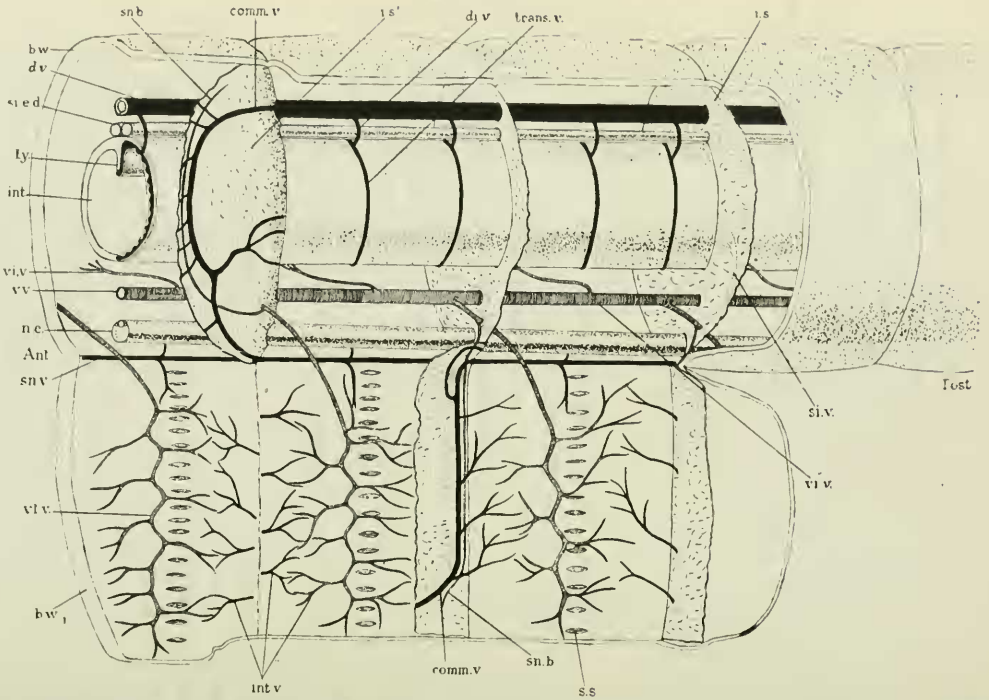
It will be seen from fig. 1 that the dorsal vessel is connected with the intestine by two pairs of dorso-intestinal vessels (*di.v.*) in each segment ; these vessels serve to establish a communication between the internal intestinal plexus and the dorsal blood-vessel (fig. 2). The anterior pair of dorso-intestinals come off from the dorsal in the anterior third of the segment, while the posterior pair lie in the posterior third, nearing the hinder septum of the segment, in close association with the so-called ' lymph-glands ' which lie on each side of the dorsal vessel in every segment here. These dorso-intestinals are very short vessels, being only about 450 μ in length, on an average. They soon enter the intestinal wall, in which they are continued as ' transverse vessels ' (vide infra).

Again, just before piercing each septum from behind, the dorsal vessel receives a commissural vessel (the dorso-lateral or the parietal vessel), which is connected ventrally with the subneural (*comm.v.*, figs. 1 and 2). This commissural vessel runs along the posterior face of each septum very near and parallel to its outer edge, i. e. the edge joining the body-wall ; and is connected with capillaries of the nephridia and the body-wall.

As I shall show later on, both the dorso-intestinal and the commissural vessels bring blood into the dorsal vessel and replenish its supply. No blood leaves the dorsal vessel in this region of the body.

2. The ventral vessel.—The ventral vessel, like the dorsal, is single throughout its length and extends from the anterior to the posterior end of the body. In the region of the intestine it has an average diameter of 115 μ and gives off a pair of ventro-tegumentary branches in each segment. Each of these branches leaves the ventral vessel just anterior to the septal wall in each segment and, after running alongside the anterior face of each septum for a little

TEXT-FIG. 1.



A diagrammatic representation of the blood-system in the region of the body behind the fourteenth segment, in the typhlosolar region of Pheretima posthuma. Five segments are shown, and the greater part of the skin of the left side of the four anterior segments has been cut and reflected out, in order to expose the blood-vessels in position. *b.w.* = body-wall; *b.w.*$_1$ = body-wall cut and reflected out; *comm.v.* = commissural vessel; *d.v.* = dorsal vessel; *di.v.* = dorso-intestinal vessel; *int.* = intestine; *i.s.* = intersegmental septum; *i.s.*^{1} = intersegmental septum turned forwards; *int.v.* = integumentary vessels; *n.c.* = nerve-cord; *si.e.d.* = supra-intestinal excretory ducts; *si.v.* = septo-intestinal vessel; *sn.v.* = subneural vessel; *sn.b.* = septo-nephridial branch; *s.s.* = setal sac; *ty.* = typhlosole; *trans.v.* = transverse vessel; *v.v.* = ventral vessel; *vi.v.* = ventro-intestinal vessel; *vl.v.* = ventro-tegumentary vessel.

distance, it pierces the septum and gets into the succeeding segment (*rt.v.*, fig. 1). Here it lies on the inner surface of the body-wall near the middle line of the segment just in front of the row of setal sacs, going right up near the mid-dorsal line (figs. 1 and 2). As it ascends along the body-wall transversely, the ventro-tegumentary vessel (*rt.v.*) gives off backwards and forwards capillaries that supply blood to the body-wall (epidermis and the muscles) and the integumentary nephridia. Besides, the septal nephridia and the prostates also receive their blood-supply from the ventro-tegumentaries. The septal nephridia are supplied by a septo-nephridial branch (*sn.b.*, fig. 1) of the ventro-tegumentary given off in each segment at the place where it pierces the septum; while the prostate glands in the segments sixteen to twenty-one receive small branches from the ventro-tegumentary in each of these segments.

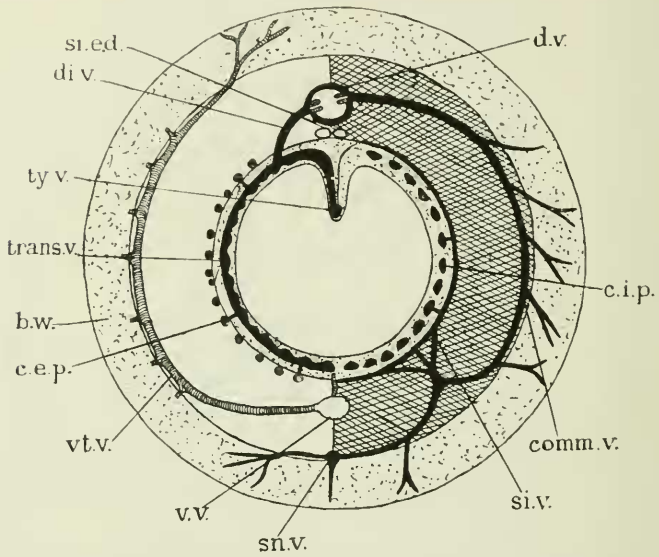
Besides the paired ventro-tegumentary branches the ventral vessel gives off dorsally a single unpaired ventro-intestinal vessel in each segment (*vi.v.*, fig. 1). This vessel originates from the ventral a little behind the middle of each segment, and runs forward to enter the ventral wall of the intestine, by three or four branches, close to the anterior intersegmental septum. The ventro-intestinal, though generally overlooked in this worm, is, however, an important vessel, and measures as much as 1·5 mm. in length in some worms from its place of origin on the ventral vessel to its place of entrance into the intestinal wall. It puts the ventral vessel into communication with the intestinal plexus. There are no valves anywhere along the course of the ventral vessel.

The ventral vessel is the main and, in fact, the only distributing channel in the intestinal region of the body. All parts in this region get their supply of blood from the ventral vessel.

3. The subneural vessel.—The subneural vessel runs along the mid-ventral line of the body-wall, being intimately attached to it, and lies, as its name indicates, beneath the nerve-cord. It is a very slender vessel and extends from the

posterior end of the worm to the fourteenth segment anteriorly, being absent from the first fourteen segments. The commissural vessel, connecting the subneural with the dorsal in the septal regions, has already been referred to above. At about the middle of each segment just in front of the line

TEXT-FIG. 2.



A diagrammatic transverse section through the region of the intestine, the right half showing a section through the intersegmental region and the left half through a segment proper passing through one of the dorso-intestinals. *b.w.* = body-wall; *c.e.p.* = capillaries of the external plexus; *c.i.p.* = capillaries of the internal plexus; *comm.v.* = commissural vessel; *d.v.* = dorsal vessel; *di.v.* = dorso-intestinal vessel; *si.v.* = septo-intestinal vessel; *s.v.* = subneural vessel; *trans.v.* = transverse vessel; *ty.v.* = typhlosolar vessel; *v.v.* = ventral vessel; *vt.v.* = ventro-tegumentary vessel.

of setal sacs, the subneural receives a pair of very small branches from the ventral part of the body-wall. One also finds in sections the subneural receiving a branch on its ventral side from the body-wall in the mid-ventral line (fig. 2).

The subneural is connected with the intestinal plexus

through the septo-intestinal (*si.v.*, figs. 1 and 2), a vessel which I describe below along with the commissural vessel.

This vessel collects blood from the small ventral part of the body-wall and the nerve-cord; and as the area over which its branches ramify is very small and the quantity of blood received is also small, the vessel itself is very slender as compared with the other longitudinal trunks.

There are no supra-intestinal vessels in this region in this worm: a pair of longitudinal ducts attached to the mid-dorsal line of the gut and described as supra-intestinal blood-vessels by Stephenson (**14**) have already been shown by me to be excretory ducts (**7**).

There are also no lateral neural vessels as found in Lumbricus.

(*b*) The Intestinal Blood-plexus.

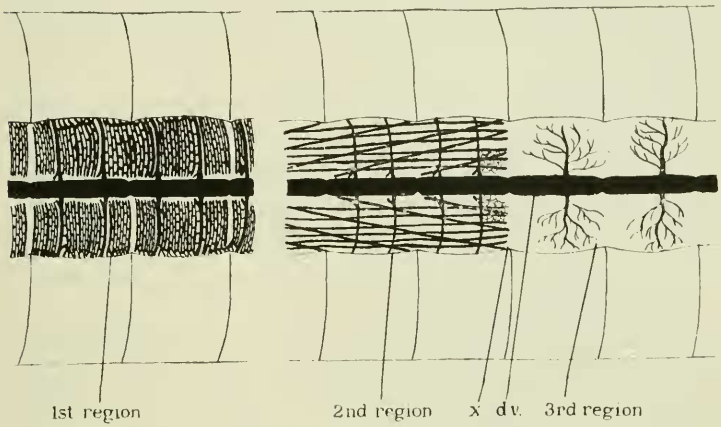
The intestinal blood-plexus (fig. 3) consists of a close network of capillaries and blood-vessels in the walls of the intestine. In Pheretima as in Megascolex (**1**) there are two capillary networks in the alimentary canal, i.e. (1) an internal deep-lying network, and (2) an external more superficial one. The internal network lies deep in the wall of the gut inside the layer of circular muscle-fibres, between it and the internal epithelial lining; while the capillaries belonging to the external network lie on the surface of the gut-wall amongst or even outside the yellow cells (chloragogen cells) which form the splanchnic layer of the peritoneal lining of the coelom. When a freshly-killed worm is opened in saline solution it is at once seen that the blood-plexus on the gut is marked out into three distinct regions—the first region is from the fourteenth to the twenty-sixth segment, where the intestinal capillaries are very thickly set and lie at right angles to the longitudinal axis of the body (transverse capillaries); the second is the longest portion and extends from the twenty-sixth segment to twenty-three to twenty-eight segments in front of the anus, the main

portion of the plexus in this region consisting of longitudinal capillaries lying parallel with one another along the intestine all round the circumference; and the third region comprises the last twenty-three to twenty-eight segments of the animal, where the blood-plexus differs markedly from what we have in the first two regions. The difference in appearance of the blood-plexus in the three regions is illustrated in fig. 3, where at the point marked *x* there is a sudden change in the arrangement of capillaries from the second to the third region. While there is a regular, almost rectangular arrangement of the capillaries in the anterior two regions of the gut, the capillaries in the posterior region (last twenty-three to twenty-eight segments) branch off in a tree-like fashion from the dorso-intestinal vessels. That the three regions mentioned above are distinct from one another will be evident from the fact, ascertained by a study of sections passing through the three regions, that in the first region (fourteenth to twenty-sixth segment) the intestinal capillaries form only the internal plexus, the external plexus being absent, that in the second region (twenty-sixth segment onwards) there are both the internal and external plexuses well developed, while in the third region (last twenty-three to twenty-eight segments) we have no internal plexus at all, all the capillaries belonging to an external plexus.

Besides the difference in the arrangement and position of capillaries in the three regions there is another feature which also distinguishes these three regions from one another, and that is the presence and absence of a typhlosole and the typhlosolar vessel. Taking the last region first, we have to note the entire absence of a typhlosole in this region. Beddard (**3**) describes the absence of typhlosole in the last few segments of Acanthodrilus, and calls this last part of the gut without a typhlosole the 'rectum'. Similarly, the typhlosole is absent in the gut in the last thirty-six segments of Lumbricus, and we can apply the term 'rectum' to these last thirty-six segments of Lumbricus and the last twenty-three to twenty-eight segments of Pheretima.

It seems reasonable to suppose that by the time the earth reaches the last rectal portion of the gut there is hardly any nutriment left in it for absorption, and hence we have the absence of the typhlosole as well as of internal blood-plexus in this region, both of these structures being the likely media for absorption of nutriment from the earth. A well-developed external network of capillaries is, however, present in the

TEXT-FIG. 3.



Semi-diagrammatic representation of the intestinal blood-plexus in the three regions of the intestine. The *1st region* extends from the fourteenth to the twenty-sixth segment; the *2nd region* from the twenty-sixth to twenty-three to twenty-six segments in front of the anus and the region includes the last twenty-three to twenty-six segments (rectal region). *d.v.* = dorsal vessel; *x* = the place where there is a change from the regular geometrical plexus to the branching tree-like plexus of the rectum.

rectal region and serves to supply blood to the wall of the gut, and also, being distributed amongst the chloragogen cells, allows the latter to take up the excretory products from the blood capillaries.

In the second region, which is the most extensive (twenty-sixth segment to twenty-three to twenty-eight segments in front of the anus) of the three regions, we have a typhlosole as well as both the internal and the external plexus equally

well developed. The internal plexus is a dense network of capillaries appearing as a sort of blood-sinus interrupted at places by the foldings of the gut epithelium (fig. 2). The typhlosolar vessel, which should be regarded as part of the internal plexus, communicates with it at two places in each segment. The external blood-plexus, which is not continuous from segment to segment, has capillaries of varying diameters. The blood apparently passes from the external to the internal plexus, as, like the case in Megascolex (1), we can see the capillaries of the external network communicating with the capillaries of the internal network at numerous places in sections.

In the first region we have only a well-developed internal plexus but no external one. Neither is there a typhlosole, although, of the specially large mid-dorsal and mid-ventral capillaries, the mid-dorsal one simulates the typhlosolar vessel.

(1) Alimentary plexus in the first region (fourteenth to twenty-sixth segment).

In this region of the gut the internal blood-plexus is best developed. The network is very dense, almost a blood-sinus interrupted at certain places ; the interspaces in the dorsal half of the plexus are very small indeed, even less than one-fourth the size of the vessels which surround them. The capillaries run parallel to one another transversely to the length of the gut, and towards the ventral half break up into capillaries of smaller calibre, so that in the ventral half of the gut a continuous blood-sinus gives place to a coarse network of capillaries. In a freshly-opened worm this region of the gut presents a very bloody appearance.

Besides the richness in capillaries of this region we have a pair of well-marked vessels lying on the dorso-lateral aspect. These begin ventrally in the intestinal plexus about the fourteenth segment, and incline gradually dorsalwards up to the twenty-sixth segment, where they join the posterior pair of dorso-intestinal vessels of that segment at the inner angles of the roots of the intestinal coeca, and also communicate at that

place with the other blood-vessels on the walls of the coeca themselves.

An equally well-developed vessel runs along the mid-dorsal line of the gut, being only a specialized capillary of the internal plexus and being also continuous with the typhlosolar vessel behind.

The external blood-plexus is almost completely absent in this region. There are, however, a few capillaries present, which can be seen attached to the outside of the gut; for example, at places where the ventro-intestinal and septo-intestinal vessels join the wall of the intestine. But they soon enter the intestinal wall and pour their blood into the internal blood-plexus; so that a regular external plexus such as we find in the second and third regions (*vide infra*) is absent in this part of the gut, the internal plexus being very strongly developed.

(2) The alimentary plexus in the second region (twenty-sixth segment to twenty-three to twenty-eight segments in front of the anus).

In this region we have both the external and internal plexuses well developed. The external plexus consists of capillaries of various sizes which are continuous on the ventral wall of the gut but not on the dorsal. They are connected with the septo-intestinals and the ventro-intestinals which apparently form their source of blood-supply. They open into the capillaries of the internal plexus as shown in fig. 2.

The internal plexus in this region of the gut presents a very regular geometrical arrangement, as shown in fig. 3. This network consists of (*a*) Longitudinal capillaries, which are very closely set around the wall of the gut, extending all along its length. They are continuous from segment to segment and number about forty all round. These capillaries form the main portion of the plexus and in transverse sections are seen to lie in the folds of internal gut-epithelium.

(*b*) Transverse Channels.—We have already mentioned that in each segment the dorsal vessel is connected with the gut by means of two pairs of dorso-intestinal vessels. These dorso-intestinals on leaving the dorsal vessel enter the

intestinal wall about $\frac{1}{2}$ mm. from their origin and go round the wall of the gut to its ventral side. I propose to apply the term dorso-intestinal to the vessel from its point of origin from the dorsal to the point of its entrance into the intestinal wall. The continuation of the dorso-intestinal on the wall of the gut I propose to call a transverse channel.[1] Corresponding to the two pairs of dorso-intestinals there are two pairs of transverse channels in each segment; each of these transverse channels is joined at its point of junction with the dorso-intestinal by a branch from the typhlosolar vessel (vide infra) (fig. 2, left half): so that these transverse channels serve to connect not only the longitudinal capillaries with each other but also the whole plexus with the typhlosolar vessel.

(*c*) Oblique Channels.—These begin at the mid-ventral line of the intestine at the intersegmental plane and run forwards and dorsalwards, passing through three segments before reaching the mid-dorsal line, where they join the typhlosolar just in front of the septa (fig. 3).

(*d*) Typhlosolar Vessel.—The typhlosolar vessel runs along the free edge of the typhlosole all down the second region of the gut (fig. 2). The typhlosole itself cannot be compared to the structure of the same name in Lumbricus, for in Pheretima it is really a bigger fold of the gut-epithelium containing not yellow cells, like those which fill up the typhlosole of Lumbricus, but only connective tissue which has the same staining qualities as the connective-tissue matrix in the layer of circular muscle-fibres of the body-wall. The typhlosolar vessel does not seem to possess a definite wall like the capillaries of the external plexus in Pheretima or the typhlosolar vessel of Lumbricus, but is only a part of the blood-sinus like the longitudinal capillaries, being, like them, in communication with the two pairs of transverse channels in each segment. We can therefore think of these transverse channels as circular ring-vessels which collect blood

[1] I have called these channels as they are thicker than the longitudinal capillaries.

from the longitudinal capillaries and the typhlosolar vessel (which we may regard as a specialized longitudinal capillary lying in the mid-dorsal line), and convey it to the dorsal vessel by means of the two pairs of dorso-intestinals in the same way as the ring-vessels of the oesophagus convey its blood to the supra-oesophageal vessel there (vide infra). It would be interesting to note here that, although the typhlosole is absent in the segments fourteen to twenty-six, there is a prominent blood-vessel in the mid-dorsal line of the gut-epithelium, the vessel corresponding to the typhlosolar behind, with which it is directly continuous.

(3) The blood-plexus in the third region (last twenty-three to twenty-eight segments).

In the last twenty-three to twenty-eight segments of the worm where the typhlosole in the gut is absent, and which region Beddard (**3**, p. 18) has referred to as the 'rectum', the intestinal plexus is different from what we have seen in the first two regions. The whole of the plexus is external, i.e. lies outside the muscular coats, there being no internal plexus. The regular and rectangular arrangement of capillaries in the typhlosolar (second) region at once changes into a branching tree-like plexus as shown in fig. 3. There is only one pair of dorso-intestinals in this rectal region in place of two pairs in the first two regions. Since there is no internal plexus the dorso-intestinals change their connexions and communicate in this region with the external blood-plexus.

The blood coming to the rectum from the ventro-intestinals and septo-intestinals goes to the external plexus, from where it passes to the dorsal through the dorso-intestinals, the part of the course involving the internal plexus having been cut out (vide infra).

(*c*) The Commissural, Integumentary, and Nephridial Vessels.

1. The Commissural Vessel.—As already mentioned, there is a pair of commissural vessels (parietal vessels) in each segment connecting the dorsal with the subneural vessel

(figs. 1 and 2). The commissural lies in the most anterior position in each segment, since the posterior face of a septum, on which this vessel lies, forms the anterior boundary of a segment. In its ventro-lateral part each commissural vessel is joined by a 'septo-intestinal' branch (figs. 1 and 2) which puts the commissural vessel in communication with the intestinal plexus, so that the commissural joins the dorsal and subneural vessels at its two ends, while in its ventral third it gives the septo-intestinal branch to the intestinal blood-plexus. It is interesting to note the Y-shaped places of junction (fig. 2) one comes across in sections, where the three limbs of the Y represent the branches of the commissural going to the dorsal and subneural vessels and the intestinal plexus respectively. All along its length the commissural vessel is joined by branches coming from the septal nephridia and the body-wall. In segments sixteen to twenty-one the commissural vessel also receives the efferent capillaries from the prostates which get their blood-supply from the branches of the ventro-tegumentaries. As shown in fig. 1. I could count in one preparation as many as eight branches entering the commissural, each of these branches being formed by the union of several branchlets.

The commissural vessel of Pheretima is a very interesting structure when we compare it with similar structures in other earthworms. Bourne (1) describes in Megascolex two vessels, which he calls 'intestino-tegumentary' and 'dorso-tegumentary', as follows: 'The main portion of the intestino-tegumentary vessel lies closely adherent to the body-wall just behind a septum, i.e. in the anterior portion of a segment', and 'the dorso-tegumentary arises in all segments regularly from the dorsal vessel immediately posterior to the septum which forms the anterior boundary of the segment in which it lies'. It is clear from this description and also from his diagram (Pl. IX, fig. 7, in his paper) that these two vessels of Megascolex run in the same transverse plane, and would thus correspond exactly to the commissural vessel of Pheretima minus its small ventral portion, since the commissural

also lies in exactly the same position. Its dorsal part with its connexions with both the dorsal vessel and the body-wall would correspond to the 'dorso-tegumentary', and its lateral part together with the septo-intestinal having connexions with the body-wall on the one hand and the intestinal plexus on the other would correspond to the 'intestino-tegumentary' of Megascolex. There being no subneural vessel in the latter genus, there is nothing in its blood-system corresponding to the ventral part of the commissural of Pheretima.

Again, the 'dorso-tegumentary' of Moniligaster (2) and Lumbricus (8) corresponds to the commissural vessel of Pheretima minus the septo-intestinal. Unlike Megascolex, these two genera (Moniligaster and Lumbricus) possess a subneural vessel like Pheretima, and we have a loop or commissural vessel connecting the dorsal with the subneural, which has been described by Jaquet (9) in Lumbricus as the 'branche dorso-sous-nervienne', a term adopted by Bourne for the same structure in Moniligaster. Jaquet also describes a 'branche tégumentaire' from the dorso-tegumentary; but I have examined the tegumentary (commissural or parietal) of Lumbricus and do not find a special 'branche tégumentaire' as Jaquet makes out. Of course, there are several branches from the body-wall (tegumentary branches) joining the commissural all along its course as in Pheretima, to which the term 'branche tégumentaire' can be applied; but the real point in which the commissural of Lumbricus and Moniligaster differs from that of Pheretima is that in the former two genera it has no connexion with the intestinal plexus, there being nothing corresponding to the 'septo-intestinal' of Pheretima.

From the comparisons made above it seems reasonable to deduce that the commissural vessel of Pheretima is a compound vessel which combines in itself the 'dorso-tegumentary' (commissural or parietal) of Lumbricus and Moniligaster (the dorso-tegumentary of Megascolex corresponding only to one of the tegumentary branches joining the commissural

in the other earthworms) and the 'intestino-tegumentary' of Megascolex. The probable homologies are set out in the following table:

1. Lumbricus	Branche tégumentaire	Branche dorso-sous-nervienne	Absent
2. Moniligaster	,, ,,	,, ,,	,,
3. Megascolex	Dorso-tegumentary	Only partially represented by the tegumentary part of the 'intestino-tegumentary'	Intestinal part of intestino-tegumentary'
4. Pheretima	One of the capillaries from the body-wall joining the dorsal portion of the commissural	Commissural vessel	Septo-intestinal.

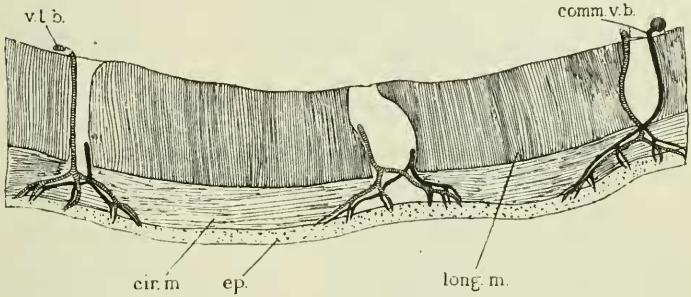
In describing the 'ventro-intestinals', of which there is a pair in each segment in Moniligaster (2, 1894, p. 330), Bourne remarks: 'They are the sole afferent vessels of the intestinal walls. There are no such vessels in Megascolex coeruleus, their function being performed by the "intestino-tegumentary" vessels.' In Pheretima we have both the 'intestino-tegumentary' (represented by the septo-intestinal) as well as the ventro-intestinal vessel in each segment; and if both are afferent vessels of the gut-wall, as I believe they are, there is a double source of supply of blood to the gut in Pheretima.

As I shall discuss later on, I believe that the course of blood in the commissural is towards the dorsal vessel. The blood from the subneural goes to the intestinal plexus through the septo-intestinal, and the branches joining the commissural all along its course bring blood into it from the body-wall and the septal and integumentary nephridia.

2. The Integumentary Vessels.—The body-wall, consisting of its muscular layers, and the epidermis receives its supply of blood from the ventro-tegumentary branches, a pair of which comes off from the ventral vessel in each segment. I have already stated that these ventro-tegumentary branches

supply the body-wall of the segment succeeding the one in which they arise from the ventral vessel (e. g. the ventro-tegumentary arising from the ventral in the fortieth segment runs along and supplies the body-wall of the forty-first segment and so on). The ventro-tegumentaries give off numerous branches backwards and forwards (fig. 1), which are distributed over the body-wall and also supply blood to the integumentary nephridia (vide infra). The ventro-tegumentaries grow thinner and thinner along their course towards the mid-dorsal line near which they end in the body-wall.

TEXT-FIG. 4.



A diagrammatic reconstruction of three serial sections showing the close parallelism of ' arterial ' and ' venous ' capillaries in the body-wall. *ep.* = epidermis ; *cir.m.* = layer of circular muscle-fibres ; *long.m.* = layer of longitudinal muscle-fibres ; *vt.b.* = a branch of the ventro-tegumentary vessel ; *comm.v.b.* = a branch of the commissural vessel.

The efferent vessels of the body-wall are the paired branches of the subneural in each segment and the numerous branches joining the commissural vessel in each segment.

The afferent and efferent capillaries run side by side in the substance of the body-wall, and can always be followed from the coelomic epithelium through the muscular layers to the epidermis. I can confirm for Pheretima Bourne's statement (2) with regard to the peripheral capillaries in Monili-gaster, that 'the most striking feature of these networks (he is speaking of capillaries in the body-wall)

is the strict parallelism which obtains throughout between " artery " and " vein " '. In serial sections it is very interesting to follow pairs of parallel capillaries in the body-wall, and one can invariably trace them to their afferent and efferent vessels. Fig. 4, reconstructed from three sections of 6 μ thickness, serves to illustrate the parallelism obtained in sections, while fig. 4 A gives an accurate camera lucida drawing of part of the body-wall mounted flat after the removal of longitudinal muscles. The strict parallelism between an 'artery' and a vein together with the capillary loops connecting them are very clearly displayed.

3. The Nephridial Blood-system.—The blood-supply of the three kinds of nephridia in Pheretima has already been described by me elsewhere (**3**), and I have nothing further to add here.

(*d*) The Dorso-intestinals and the Ventro-intestinals.

The Dorso-intestinals.—I have referred to these vessels already in describing the dorsal vessel. The dorso-intestinals form, so to speak, the efferent vessels (veins) of the intestinal blood-plexus, as all the blood in the intestine is returned to the dorsal vessel through these dorso-intestinals. There is a single pair of them in the fourteenth segment and in all the segments of the rectal (post-typhlosolar) region, while in the remaining large part of the intestine we have two pairs to each segment. We have already noted that the dorso-intestinals communicate with the external plexus in the rectal region but with the internal plexus in the first and second regions. At the place where the dorso-intestinal leaves the gut, it also receives a branch from the typhlosolar vessel (fig. 2).

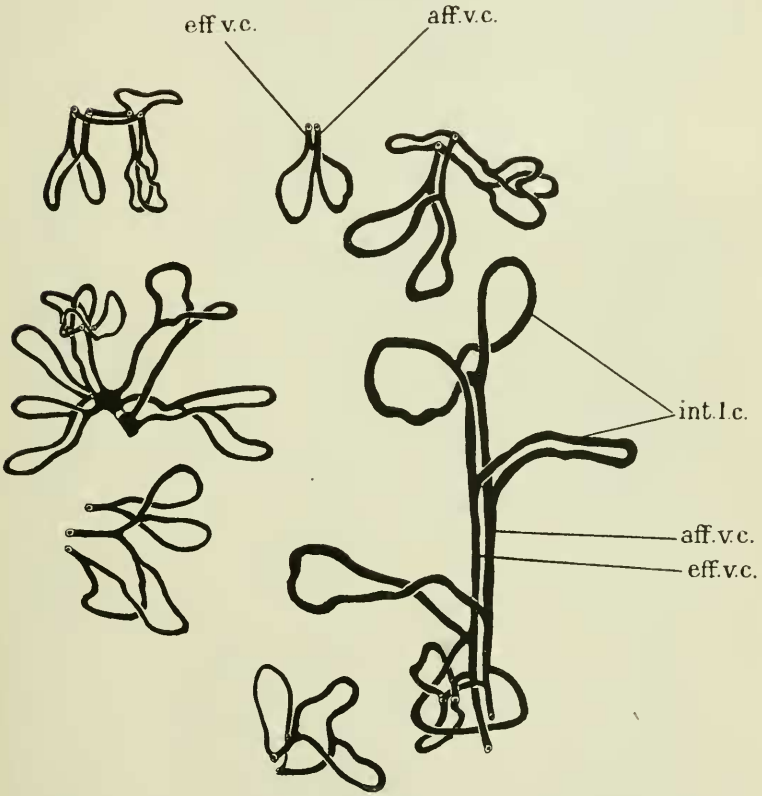
The Ventro-intestinals.—These single unpaired vessels in each segment have also been referred to above. They form the afferent vessels (arteries) of the gut, and are present in all the three regions.

3. The Blood-system in the First Fourteen Segments.

In the first fourteen segments the blood-system is highly modified on account of the cephalization of this region, and differs a good deal from the system in the general body-region.

Amongst the longitudinal trunks the subneural as such is

Text-fig. 4 A.



Disposition of blood-capillaries in the body-wall from a whole mount of a portion of the body-wall treated with caustic potash, showing how a 'venous' capillary passes into an 'arterial' one. *aff.v.c.* = capillary of the afferent vessel; *eff.v.c.* = capillary of the efferent vessel; *int.l.c.* = capillary loop connecting the afferent and efferent vessels.

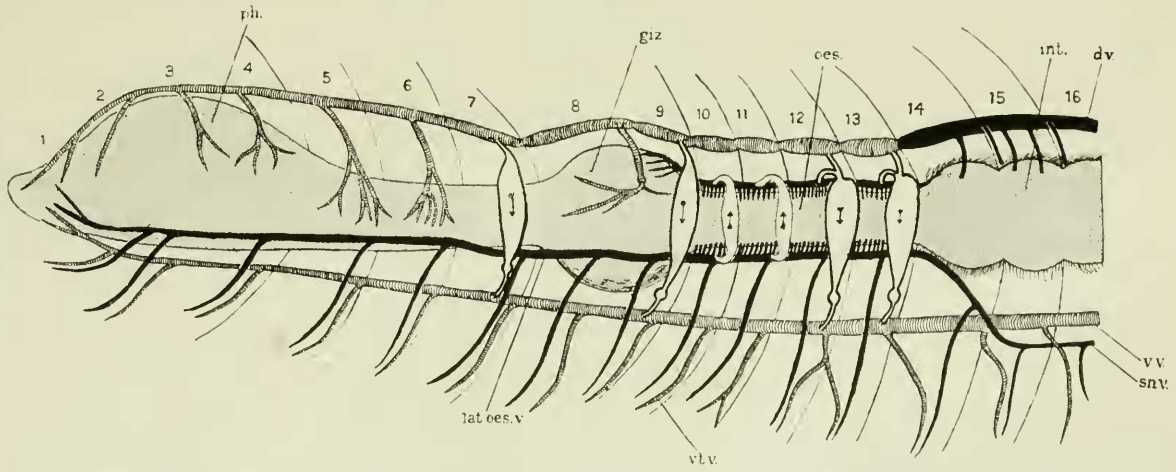
absent ; it bifurcates in the fourteenth segment, and the two branches curve round (fig. 5) the nerve-cord to be continued into the two lateral oesophageal vessels. A new large vessel in this region limited in extent is the supra-intestinal vessel, which is closely attached to the oesophagus in the mid-dorsal line and communicates freely with the blood-plexus of the oesophagus. Besides these there are the big pulsating ' hearts ' in many of the segments of this region, by means of which the dorsal vessel pumps out all the blood it receives either into the ventral vessel to be distributed by it or directly to the various organs in this part of the body.

(*a*) The Longitudinal Trunks.

1. The Dorsal Vessel.—The dorsal vessel continues in front up to the third segment, where it divides into three branches near the cerebral ganglion, these branches being distributed over the pharyngeal mass and the wall of the buccal cavity. While in the region of the intestine the dorsal vessel lies close upon the gut, being connected with it by two pairs of dorso-intestinals ; in this anterior region it is removed considerably away from the oesophagus. Except in the fourteenth segment, where the dorsal vessel is connected by a single (not two) pair of dorso-intestinals, there are no such venous branches at all in the anterior cephalized region. Since there is no subneural vessel in this region the commissural vessels connecting the dorsal with the subneural in the intestinal region are absent in this anterior region. However, the dorsal vessel here gives off, in many segments, pulsatile vessels called the ' hearts '. These structures I shall describe separately below.

The intersegmental valves present in the posterior part of the dorsal vessel are present here also, and have the same structure and disposition, making the blood flow in the anterior direction. But the valves at the orifices of the dorso-intestinals and commissurals into the dorsal (*vide infra*) in the posterior region have no counterpart here ; in their place there are other valves away from these orifices, leading the blood outwards from the dorsal vessel.

TEXT-FIG. 5.



A semi-diagrammatic representation of blood-vessels in the first sixteen segments of Pheretima. *d.v.* = dorsal vessel; *giz.* = gizzard; *int.* = intestine; *lat. oes.v.* = lateral oesophageal vessel; *oes.* = oesophagus; *ph.* = pharynx; *sn.v.* = subneural vessel; *v.v.* = ventral vessel; *vt.v.* = ventro-tegumentary vessel. The 'latero-intestinal' hearts are in the twelfth and thirteenth segments, the 'lateral' hearts in the seventh and ninth segments, while the tenth and eleventh segments contain the 'anterior loops'.

2. The Supra-intestinal Vessel.—The supra-intestinal vessel, which is confined to the oesophageal region behind the gizzard, occupies the same relative position with regard to the gut as the dorsal vessel does in the region of the intestine. It lies beneath the dorsal vessel rather closely attached to the dorsal wall of the oesophagus, while the dorsal vessel itself is removed considerably away from the gut. It is usually double along its whole extent, but the two halves come together and communicate with each other at several places. The supra-intestinal vessel extends from the tenth to the thirteenth segment. In the tenth and eleventh segments it communicates with the lateral oesophageal vessels by large commissural vessels or 'loops' that go round free from the wall of the oesophagus; while in the twelfth and thirteenth segments it communicates with the ventral vessel through the 'hearts'. The vessel ends anteriorly by breaking up into capillaries in front of the tenth segment, and these capillaries are distributed over the walls of the oesophagus and the gizzard. Posteriorly the vessel ends by joining the posterior pair of 'hearts' in the thirteenth segment, although a slender branch very often continues backwards on the mid-dorsal line of the gut for a segment or two.

The supra-intestinal is the efferent vessel for the gizzard and the oesophagus, and all the blood brought in it from these structures is no doubt carried into the 'hearts' of the twelfth and thirteenth segments.

3. The Ventral Vessel.—The ventral vessel extends anteriorly up to the second segment, and in each segment gives off a pair of ventro-tegumentary branches as in the posterior region, with the difference that the branches from a particular segment are spread over and distribute blood to the body-wall, the septa, and the nephridia in the same segment and not the succeeding one, as they do behind. All the special organs in this part of the body, e.g. the spermathecae, the seminal vesicles, the ovaries, and the oviducts are supplied with blood by little branches from the ventro-tegumentaries. The vessel ends anteriorly in a pair of branches

in the second segment. There are no ventro-intestinals in this region of the body.

4. Lateral-oesophageal Vessels.—These are a pair of fairly large vessels in the first fourteen segments of the animal situated on the ventro-lateral aspect of the oesophagus. They are always found full of blood and can be easily seen. Behind the gizzard, i.e. in segments ten to thirteen, they are very intimately attached to the wall of the oesophagus and, as can be seen in sections, communicate with the oesophageal ring-vessels throughout these four segments by as many branches as the number of ring-vessels. In the region of the gizzard and in front, however, they are free from the wall of the gut, but receive a branch in each segment from the wall of the gut.

The lateral oesophageals receive in each segment a pair of branches that bring back blood not only from the body-wall and septa of this region but also from the seminal vesicles and the spermathecae. They thus function here like the branches of the subneural and commissural vessels behind, which collect blood from the body-wall, the nephridia and other organs in coelom like the prostates.

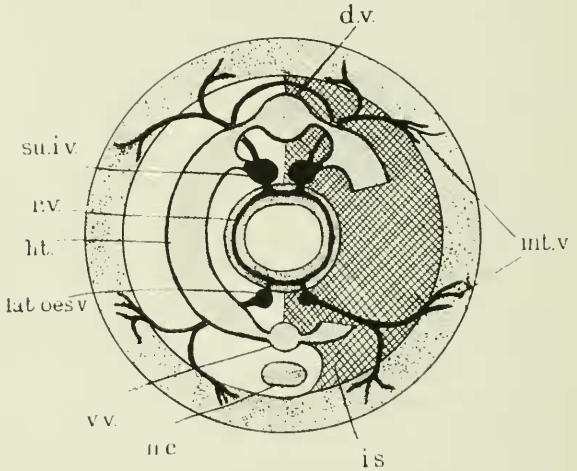
It only remains to be added that the lateral oesophageals are a continuation forward of the subneural vessel. In the fourteenth segment the subneural vessel forks into two, and each of the two branches loops round the nerve-cord and comes to lie dorsal to it and is continued forward along the ventro-lateral aspect of the oesophagus as the lateral-oesophageal vessels.

(*b*) The 'Hearts' and the Anterior Loops.

It will be seen from what we have described above that there is no direct communication between the dorsal and ventral vessels in the region of the body behind the thirteenth segment, but in the anterior thirteen segments the dorsal vessel communicates directly with the ventral through the 'hearts' in the seventh and ninth, and twelfth and thirteenth segments. It is only these four pairs of 'hearts' that are connected with the ventral vessel; but, besides these, there are other 'hearts'

which are also pulsatile but supply blood to some of the organs directly, e.g. the gizzard and the pharyngeal nephridia. I have adopted Bourne's suggestion (1, p. 64 n.) of naming all rhythmically contractile, circularly disposed vessels as 'hearts', which term thus includes even the anterior branches of the dorsal vessel which do not join the ventral vessel.

TEXT-FIG. 6.



A diagrammatic transverse section of the earthworm through the region of the 'latero-intestinal' hearts. In the right half is shown the intersegmental septum just behind the 'heart'. *d.v.* = dorsal vessel; *ht.* = latero-intestinal heart; *i.s.* = intersegmental septum; *int.v.* = integumentary vessels taking blood (venous) to the lateral oesophageals and the supra-intestinals; *lat.oes.v.* = latero-oesophageal vessels; *r.v.* = a ring-vessel in the oesophagus; *su.i.v.* = supra-intestinal vessel; *v.v.* = ventral vessel.

Again, Bourne (1, p. 64 n.), following Perrier, distinguishes 'lateral hearts' from the 'intestinal hearts' according as they are connected dorsally with the dorsal or supra-intestinal vessels. The 'hearts' in the twelfth and thirteenth segments in Pheretima communicate dorsally with both the dorsal and supra-intestinal vessels and are therefore 'latero-intestinal' hearts, while the 'hearts' in the seventh and ninth segments belong to the category of 'lateral hearts'. Coming to the 'loops' of the tenth and eleventh segments, we find that they

communicate dorsally with the supra-intestinal vessel, while ventrally they are connected with the lateral-oesophageal vessels. They might have been called ' intestinal hearts ' but for the fact that these ' loops ' do not pulsate, have non-muscular walls unlike those of the ' hearts ', and I believe that the flow of blood in them is from the lateral oesophageals to the supra-intestinal, a fact which I refer to again below. On these considerations I exclude these vessels from the category of ' hearts ' and call them ' anterior loops ', since they have nothing in common with the so-called ' hearts ' and ' anterior loops ' in greater detail below ; they are shown in fig. 5.

Thirteenth and Twelfth Segments.—In each of these two segments there is a pair of ' latero-intestinal ' hearts. In systematic accounts of the genus Pheretima it is only these two pairs that are described, and no mention is made of the anterior pairs of ' hearts '. Even if the term ' hearts ' be restricted to those commissures which communicate with the ventral vessel below it should include the ' hearts ' of the seventh and ninth segments. This diagnostic character for the genus Pheretima is thus generally erroneously described, and the genus should be recognized to possess at least four pairs of ' hearts ', two ' lateral ' and two ' latero-intestinals '.

The ' hearts ' of the twelfth and thirteenth segments (fig. 5) are situated in the posterior parts of these two segments, and their walls are intimately attached to the septa behind them. They have thick muscular walls and a spacious cavity, and at their dorsal ends communicate anteriorly with the supra-intestinal and posteriorly with the dorsal vessel. At the places where the branches from the dorsal and supra-intestinal meet to enter the ' heart ', each has a pair of valves leading to the ' heart ', and similarly there is a pair of valves at the ventral end of each ' heart ' just above the place where it joins the ventral vessel (fig. 11). The dorsal valves prevent the blood from going back to the dorsal or supra-intestinal vessels during systole, while the ventral valves prevent the blood from entering the ' heart ' from the ventral vessel during diastole.

Eleventh and Tenth Segments.—These two segments contain no ' hearts ', but each of them has a pair of commissural vessels connecting the supra-intestinal with the lateral oesophageal of each side. These vessels lie in the posterior parts of these segments near their posterior septa, and are partially covered by the latter. Unlike the ' hearts ' these ' loops ' of the tenth and eleventh segments are thin-walled, their walls being non-muscular, and they have no valves anywhere along their length.

The blood, by means of these ' loops ', flows from the lateral-oesophageals into the supra-intestinals. The latter collect blood from the gizzard and oesophagus and also receive blood in these two segments directly from the lateral oesophageals. All this blood they carry into the ventral vessel through the ' hearts ' in the twelfth and thirteenth segments.

We may note here that the lateral oesophageals in Lumbricus pour their blood into the dorsal vessel in the tenth segment and into the large parietal in the twelfth.

Ninth Segment.—In the ninth segment there is a pair of ' lateral hearts ' connecting the dorsal with the ventral vessel. This pair of ' hearts ' is generally asymmetrical. the left ' heart ' being large and well developed as compared with the small thin-walled and ill-developed one of the right side, which, however, sends a branch to the oesophagus in this segment. The ' heart ' on the left side has valves pointing downwards along the greater part of its length, and there is also a pair near the point of opening of the ' heart ' into the ventral vessel. There are altogether four pairs of valves and their position and arrangement is illustrated in fig. 11 A.

Eighth Segment.—In the eighth segment the dorsal vessel gives off a pair of large thick-walled branches which do not join the ventral vessel but on account of their contractility are still called ' hearts ' ; each of them presents a bulb-like dilatation at some distance from its origin and immediately forks into two (fig. 5), the posterior branch going to the septum and body-wall, and the anterior dividing and distributing blood over the wall of the gizzard in a large number of capil-

laries which run longitudinally parallel to one another. These branches of the dorsal vessel have a series of paired valves along their length between the point of their origin and the place where there is the bulb-like dilatation. The bulb-like dilatation which occurs at the distal end of all the 'hearts' contains a pair of thick valves pointing away from the dorsal and towards the ventral vessel, as shown in fig. 11.

The blood to the gizzard, therefore, is supplied from the dorsal vessel by the pair of branches in this segment; while the capillaries of the supra-intestinal vessel, which has its beginnings here, collect blood from the gizzard and take it into that vessel.

Seventh Segment.—In the seventh segment there is a pair of 'lateral' hearts, each of which is joined below both with the ventral and the lateral oesophageal vessels, which latter are themselves joined together by a cross channel. In its upper part each of this pair of 'hearts' is thick-walled and has valves leading blood outwards, but in its ventral part each 'heart' is thin-walled and has also no valves in it. There is no doubt that the blood flows from the dorsal to the ventral vessel; but it seems probable that the supply of blood in the ventral vessel, which is very thin in this region and contains little blood, is also replenished from the lateral oesophageals, which are always large and full.

Sixth, Fifth, and Fourth Segments.—In the sixth segment, and also in the fifth and fourth, there is a pair of branches given off from the dorsal vessel each of which has a pair of valves leading outwards near its origin, and supplies blood to the masses of pharyngeal nephridia in each of these three segments. These branches are also pulsatile and can therefore be named 'hearts'.

Third Segment.—In the third segment before the dorsal vessel breaks up anteriorly, it gives off a pair of branches to the pharyngeal mass behind the cerebral ganglion. These branches also possess valves near their origin which direct the flow of blood outwards.

(*c*) The Blood-vessels of the Gut in the first Fourteen Segments.

In segments ten to fourteen there are in the oesophageal wall a series of very definite and striking transverse vessels, about twelve pairs per segment, joining the supra-intestinal above and the lateral oesophageals below; the breadth of these vessels is at least equal to the intervals between them. They are not united by longitudinal connexions and are continuous across the mid-ventral line. These ring-vessels (fig. 6) are very characteristic of the oesophagus behind the gizzard, and are situated inside the muscular coats of the oesophagus. In this region both the lateral oesophageals and the supra-intestinals are intimately attached to the oesophagus, and the blood flows from the former into the latter through these transverse ring-vessels, the latter receiving no supply at all from the ventral vessel.

In the eighth and ninth segments the gizzard receives its supply of blood from the 'hearts' of the eighth segment, the branches of which divide and run along the outer wall of the gizzard in about fourteen parallel longitudinal capillaries. There is a second set of parallel capillaries which collect blood from the gizzard and join the supra-intestinal vessel.

In front of the gizzard, i.e. in the first seven segments, the pharynx and the oesophagus get their supply of blood from the 'hearts' of the dorsal vessel, and branches of the lateral oesophageals collect blood and take it to the latter from this part of the gut.

4. Comparison with the Blood-system of the Lumbricidae.

In main outline the arrangement of blood-vessels in *Pheretima* resembles that of *Lumbricus* and *Allolobophora*, the latter more than the former. The main longitudinal trunks—the dorsal, the ventral, and the subneural—are the same in the three genera, but in *Lumbricus* there are also in addition the two lateral neurals which are absent in the

other two genera. Moreover, while in Lumbricus and Allolobophora the subneural goes right up to the anterior end of the body, in Pheretima it passes into the lateral oesophageals in the fourteenth, as it also does in Moniligaster (2), being absent in the first thirteen segments. The venous branches of the dorsal vessel bringing blood into it behind the 'hearts' are the 'dorso-intestinals' and the 'commissurals'. The latter, while they lie completely in one segment in Pheretima, occupy two segments in Lumbricus and Allolobophora. In these the ventral portions of the commissurals lie on the posterior face of a septum in one segment, while the dorsal portions lie on the anterior face of the same septum in the segment in front. In this way, while the commissural vessel enters the dorsal vessel in front of a septum, it enters the subneural immediately behind that septum; but in Pheretima, both the ends of the commissural and, in fact, the whole of the commissural, lies on the posterior face of a septum.

The ventro-tegumentaries in all the three genera arise in the segment anterior to the one they supply; but while in Pheretima and Allolobophora the ventro-tegumentary runs along the middle line of a segment (fig. 3), it runs very near the anterior septum alongside the commissural in Lumbricus. The parallelism between an artery and vein shown in fig. 4 in Pheretima in the body-wall is not found in Lumbricus, in which the arterial branch lying inside the muscular layers of the body-wall takes a dip towards the epidermis, runs beneath this layer for a short distance, and runs back to the muscular layers to be continued as a venous branch to the commissural into which it enters (6).

As regards the blood-vessels in connexion with the gut we may notice the absence of septo-intestinal vessels in the Lumbricidae, whereas in Pheretima the gut has a double source of blood-supply (the ventro-intestinals and the septo-intestinals); in the other two genera it gets all its blood from the ventral vessel only. The typhlosopar vessel of Pheretima, unlike that of the Lumbricidae, is only

a specially developed mid-dorsal portion of the gut-plexus, and has no definite walls of its own, nor does it communicate directly with the dorsal vessel as it does in Lumbricus.

In the anterior cephalized region of the body besides the differences in the number and position of the 'hearts', there is the presence in Pheretima of an additional 'supra-intestinal vessel' which receives all the blood from the lateral oesophageals and pours it into the 'hearts'; while in the other two genera, the blood from the lateral oesophageals goes directly to 'hearts', and there is no 'supra-intestinal' vessel.

5. The Course of the Circulation of the Blood.

All observers are agreed upon the fact that the blood-current in the dorsal vessel has a forward direction. I have already stated that just in front of each septal plane, where the dorsal vessel is very much constricted and has the narrowest lumen, there are forwardly-directed valves which, when the vessel contracts, prevent the flow of blood backwards. These inter-segmental valves, as we may call them, form an incomplete circular ridge on the internal wall of the vessel at their point of origin; but it can easily be seen that the valves consist of two large dorso-lateral valves, while there are small dorsal and ventral ones (figs. 7 and 10). These valves are more or less continuous with one another, so that we can regard them as constituting one valve with small dorsal and ventral lobes and large lateral lobes. The large dorso-lateral lobes project forwards into the lumen of the vessel for some distance, and are seen as two masses lying free in the dorsal vessel in transverse sections. Fig. 10 (*a*, *b*, and *c*) shows the disposition of this intersegmental valve in serial sections. In Lumbricus, on the other hand, there are two large lateral valves, as shown by Johnstone (**9**), in the same position and having the same function.

The dorsal vessel receives two pairs of dorso-intestinals and one pair of commissurals ('parietals' or 'dorso-sous-nerviens') in each segment behind the fourteenth. The

question is, what is the course of blood in these two kinds of vessels? Does the blood come into the dorsal from both or from only one? According to Bourne (**1**, p. 74) and Vejdovsky (**11**, p. 115), the blood flows from the intestinal capillaries into the dorsal vessel through the dorso-intestinals, and in this I agree with them. In recently-killed worms I have cut these dorso-intestinals to see from which of the cut ends the blood flows, and I have invariably found blood oozing out from the side of the intestinal capillaries. Moreover, the arrangement of valves which I refer to later confirms this view. With regard to the course of blood in the commissural vessel ('dorso-tegumentary' of Bourne in Moniligaster), I believe with Perrier (as quoted by Bourne in **1**) and Benham (**1**, p. 255) that blood enters the dorsal vessel from these commissurals. Bourne (**1**, p. 75), however, believes that blood leaves the dorsal vessel by the dorso-tegumentaries. But later on in his paper on Moniligaster, after discussing the point in an elaborate manner (**2**, p. 335) and concluding that Benham's view is incorrect and that blood flows outwards from the dorsal by the dorso-tegumentaries, he adds (**2**, p. 336), 'the peripheral capillaries in the region of the body behind the hearts are also supplied, to an extent which probably varies from time to time and is, I expect, never very great, from the dorsal vessel by means of the dorso-tegumentary vessels.' Further on in the same paper (p. 350), while generalizing on the vascular system of earthworms, Bourne refers again to the course of blood in the dorso-tegumentaries (commissurals) and says, 'I have again and again returned to the course taken by the blood in these vessels (dorso-tegumentaries). I cannot help thinking that primitively they are efferent vessels, and that both they and the dorso-intestinal vessels bring blood to the dorsal vessel. In this case they can only have, in worms otherwise well provided with a venous system, the function suggested above for Moniligaster grandis of regulating the pressure in the peripheral capillaries, and have practically no flow in them in one direction or the other.' Bourne here seems to give away his case

for the course of blood in the dorso-tegumentaries, and I am convinced that his statement with regard to the primitive condition that I have quoted above holds for adult Pheretima, and in fact all earthworms. Both by a study of the disposition of valves, and by cutting the commissurals and observing from which of the cut ends the blood flows, I am convinced that blood flows into the dorsal vessel from the commissural vessels as it does in the case of the dorso-intestinals. In fact I believe that the dorsal vessel all along the body of the worm behind the first thirteen cephalized segments is a channel only for collecting blood and propelling it forwards. It gives out no blood at all behind the thirteenth segment as it receives none in the first thirteen segments; so that we have two clearly marked divisions of the dorsal vessel—the large posterior division of it behind the 'hearts' being the collecting channel, and the anterior short division of the first thirteen segments being the channel for distribution of all the blood collected behind.

As regards the disposition of the valves situated at the entrance of the dorso-intestinals and the commissurals into the dorsal, they are easily seen in transverse sections projecting into the lumen of the dorsal vessel. In two lucky preparations of the dorsal vessel, in which the latter was torn open and fixed with the valves projecting out into the open lumen, I have been able to see the valves displayed in an admirable manner. They are shown in fig. 7. The valves are seen in two conditions, i.e. either protruding inwards into the lumen of the dorsal vessel or flush with the wall of the vessel. In the former condition they are more or less conical in shape, the blunt apex of the cone forming the projecting end into the dorsal vessel, and the base being continuous with the wall of the vessel; in the latter condition there is nothing projecting into the lumen of the dorsal vessel, and the valves look like closed sphincter muscles in the wall of the vessel, the actual valves being contained in the upper ends of the dorso-intestinals or commissurals. There can be no doubt that these two conditions of the valves represent them as they are during the

diastole and systole of the dorsal vessel projecting inwards when the dorsal vessel is filling and the blood is coming in through both the dorso-intestinals and the commissurals, and lying flush with the wall with the apertures closed when the dorsal vessel contracts.

Bourne (2, p. 334) says, 'In Moniligaster as in Megascolex, while there are valves which would mechanically

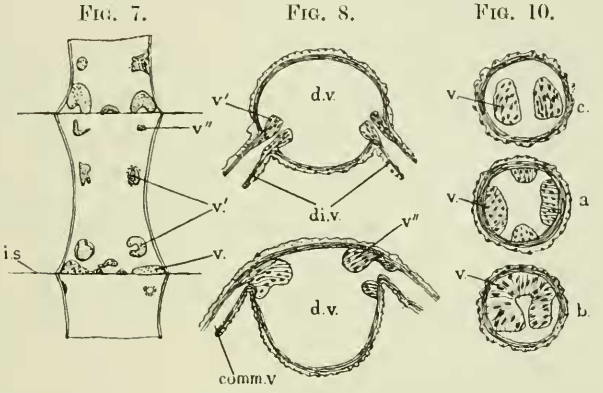


Fig. 9.

Text-Fig. 7.—Portion of the dorsal vessel cut open along its median dorsal line showing the valves in its lumen. *v.* = the valves at the intersegmental septa; *v'.* = valves at the entrance of the dorso-intestinals into the dorsal; *v''.* = valves at the entrance of the commissural vessels into the dorsal.

Text-Fig. 8.—Section of the dorsal vessel passing through the region where the dorso-intestinals enter the dorsal vessel showing the valves at the entrance. *d.v.* = dorsal vessel; *di.v.* = dorso-intestinal vessel.

Text-Fig. 9.—Section of the dorsal vessel showing the valves at the entrance of the commissural vessels into the dorsal. *d.v.* = dorsal vessel; *comm.v.* = commissural vessel.

Text-Fig. 10.—Three sections of the dorsal vessel showing the intersegmental valves. *a.* = about the place of origin of the valve; *b.* = a little in front; *c.* = still further forward.

prevent blood flowing into the dorso-intestinal vessel from the dorsal vessel, there are no such valves where the dorso-tegumentary vessels join the dorsal vessel. I have, however, observed in Moniligaster and some other worms a sphincter muscle in the wall of the dorso-tegumentary vessel close to its

origin.' As a matter of fact the valves at the point of entrance of both the dorso-intestinals and the commissural vessels (dorso-tegumentaries) look like sphincter muscles when they are not in the protruding position and are flush with the wall of the dorsal vessel. It is not unlikely that the sphincter muscles seen in Moniligaster by Bourne are really the valves in the closed condition, which, like those of the dorsal vessel, have the form of circular ridges. In transverse sections of Pheretima they are seen as small club-shaped structures, attached to the inner wall of the commissural vessel just where the latter narrows to join the dorsal vessel, and having their broad ends projecting freely into the cavity of the dorsal vessel (fig. 9). Johnstone (**8** and **9**) describes a similar disposition of valves in Lumbricus both in the dorso-intestinals and the commissurals, and I have verified it from my sections of Lumbricus. The disposition of valves and the course of blood-flow in these two vessels are therefore similar in both the worms (Lumbricus and Pheretima) and probably in all earthworms.

Another fact, which confirms my view with regard to the flow of blood into the dorsal vessel from the commissural (dorso-tegumentary) and not vice versa, is that in dissections of the fresh worm when the flaps of body-wall are pinned down after a mid-dorsal incision, the commissural vessels are almost always torn off from the dorsal vessel near their point of entrance into the latter, and the blood oozes out not from the dorsal vessel or the portion of the commissural left attached to it, but always from the cut end of the commissural near the outer edge of the flaps. This shows that the direction of blood is towards the dorsal and not away from it. If the flow of blood were from the dorsal to the commissurals, we should see the dorsal emptying itself through the upper cut pieces of the commissurals, especially since the dorsal vessel keeps pulsating for some time after the worm is opened in the salt solution. As a matter of fact no blood oozes out of the dorsal, which remains full.

Moreover, leaving aside the question of valves and the

flow of blood from cut ends, I think Bourne's view that blood in the commissural vessel comes out of the dorsal and flows towards the subneural is untenable even on theoretical grounds. He is agreed on the fact that branches joining the commissural vessel are veins bringing blood to it from the body-wall and the nephridia, and shows them as such in his diagrams (Pl. 26, fig. 34, 2); but he believes that all the blood is collected in the subneural and passes forwards along the lateral longitudinals (lateral oesophageals) to enter the posterior pair of 'hearts'. Assuming for a moment that Bourne's view is correct (although I do not agree with it) and that the blood from the subneural goes all the way to the hearts, why should any part of this blood come from the dorsal in each segment via the commissurals? If the commissural is a collecting channel for all the blood from the body-wall and the nephridia, why should it get any blood at all from the dorsal vessel? There is no meaning in the blood coming from the dorsal into the subneural in each segment and then entering the 'hearts', while it could do so by going into the 'hearts' straight along the dorsal vessel. It is to obviate this difficulty that Bourne takes the view that the commissurals have practically no flow in them in one direction or the other and that they regulate the pressure in the peripheral capillaries—a supposition which is easily disproved by cutting the commissurals and seeing that blood *does* flow in them towards the dorsal vessel.

As a matter of fact, so much blood leaves the dorsal vessel anteriorly through the 'hearts', of which there are four in *Pheretima* connected with the ventral vessel and others supplying the organs directly, that it is difficult to conceive on *a priori* grounds that any blood leaves the dorsal vessel at all behind the thirteenth segment.

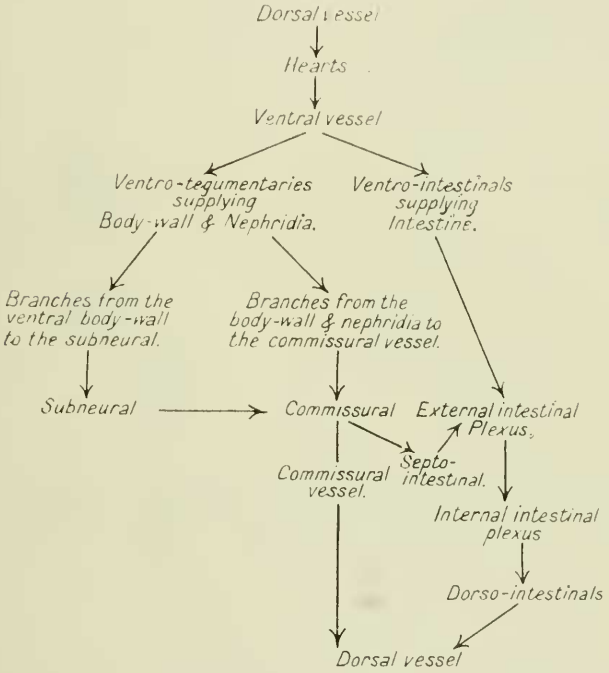
Having decided that the dorsal vessel all along the body behind the thirteenth segment is only a channel for collection and propulsion forwards of the blood which enters it from the intestinal network and the commissural vessels, the rest of the circulation in the worm becomes easy to follow.

The ventral vessel is the chief distributing channel and, so to speak, the arterial trunk of the body. All observers are agreed that blood flows backwards in this vessel in the region of the body behind the 'hearts', and that the blood is distributed to the body-wall and the other organs lying in the body-cavity (nephridia (septal and integumentary), nerve-cord, prostates, &c.) by means of the pair of ventro-tegumentaries in each segment, and to the gut by means of a single unpaired ventro-intestinal. Every structure in the body region in fact gets its supply from the ventral vessel.

The subneural vessel collects blood from the ventral part of the body-wall and the nerve-cord by means of a pair of small branches it receives in each segment. All this blood goes into the commissural vessels, from which part of it goes to the intestine through the septo-intestinal and the rest to the dorsal all along the commissural, the latter receiving the greater part of its blood-supply from the capillaries that enter into it from the body-wall and the nephridia all along its length. The flow in the subneural is therefore from in front backwards. This can be easily seen by pinching or cutting the vessel in a narcotized worm and watching the direction of blood-flow.

It should be noted that the intestine has a double supply—one from the ventral through the single ventro-intestinal, and the other from the subneural through a pair of septo-intestinals in each segment; this is what we should expect considering the large amount of blood in the extensive network of capillaries on the gut-wall. In *Lumbricus* the only source of blood for the gut is the ventral vessel; but there the gut receives two or more ventro-intestinal branches in each segment, while in *Pheretima*, there being only one unpaired ventro-intestinal vessel in each segment, the amount of blood supplied to the gut from the ventral vessel is comparatively small, and I suppose it is to supplement this that we have blood brought to the gut by the septo-intestinals. Both the ventro-intestinals and septo-intestinals bring blood to the external intestinal plexus from which the blood passes into the internal intestinal plexus. From the internal plexus

he blood finally passes into the dorsal vessel through the two pairs of dorso-intestinals in each segment. In the posterior region of the gut—the post-typhlosolar or the rectal region, however, the blood brought to the external plexus passes directly into the dorsal vessel through a single pair of dorso-intestinals in each segment, which, as already mentioned, communicate with the external plexus, the internal plexus being absent in this region. The course of blood in the intestinal region can be shown diagrammatically as follows :—



It will be seen that the ventral vessel and its branches, the ventro-tegumentaries and ventro-intestinals, form the arterial vessels, while the subneural, the commissurals, the dorso-intestinals, and the dorsal vessel itself are the chief veins (using the word in an anatomical sense) in the worm. The blood in the dorsal vessel in a certain segment must go to the ' hearts ', and return by the ventral vessel into that segment

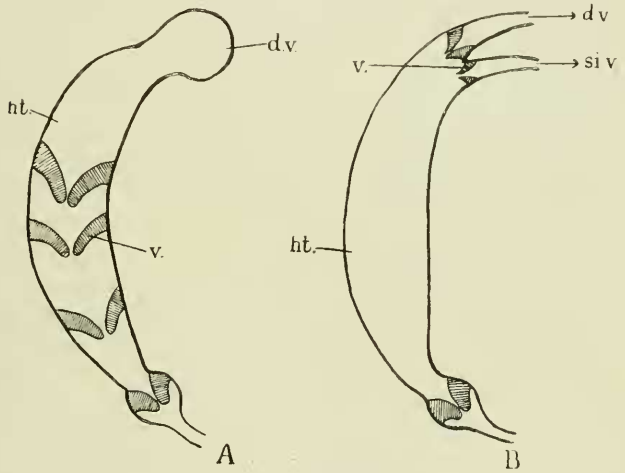
again—so that the blood-flow is not self-sufficient in one segment ; the blood must circulate in the whole body.

In the first thirteen segments (fig. 5) the blood-system is different, and so is the course of blood. The dorsal vessel is no longer a receiving channel ; it has no dorso-intestinals and commissurals opening into it and feeding it with blood—in fact it receives no blood at all, but behaves instead as a great arterial trunk, pumping out all the blood it has received in its posterior region. Of course the greater part of its blood, together with the whole of the blood in the supra-intestinal vessel, is pumped into the ventral vessel through the two pairs of ' latero-intestinal hearts ' in the twelfth and thirteenth segments. But a quantity of blood flows forwards anteriorly and this is pumped into the ventral vessel by means of the ' lateral hearts ' of the ninth and seventh segments, and is supplied to the gizzard and the pharyngeal nephridia by the ' hearts ' in the eighth and fourth, fifth and sixth segments, until the dorsal vessel ends by branching on the pharyngeal mass. In accordance with the change of function of the dorsal vessel we have the change in the disposition of the valves. In this region there are no valves projecting into the lumen of the dorsal vessel ; on the other hand, the valves are present in all the ' hearts ' at a little distance away from their origin from the dorsal vessel. These valves point in the direction away from the dorsal vessel, and lead the blood from the dorsal vessel outwards, preventing any blood taking the reverse course. There are also valves at the distal ends of the ' hearts ' (fig. 11) which allow blood to flow out of ' hearts ' during systole, but do not let the blood come back during diastole. The dorsal vessel is therefore a distributing channel here ; most of its blood it pumps out into the ventral vessel for distribution, but a small quantity it distributes itself to the gizzard, the pharyngeal nephridia and the pharynx.

With regard to the flow of the blood in the ventral vessel, I agree with Bourne (**1**, p. 77) in thinking that the blood coming from the ' hearts ' flows both forwards and backwards. There are no valves in the ventral vessel preventing blood from flowing anteriorly, and in addition to the ' hearts ' of the twelfth and

thirteenth segments there are 'hearts' in the ninth and seventh segments also to take blood into the ventral vessel. I also agree with Bourne (1) when he says, 'All the blood which enters the ventral vessel comes from the "hearts", and that all the ventro-integumentary branches—those anterior to the "hearts", as well as those posterior to them—are efferent vessels. So far as the ventral vessel is concerned, they carry blood away from it.' The ventral vessel, therefore, here as in

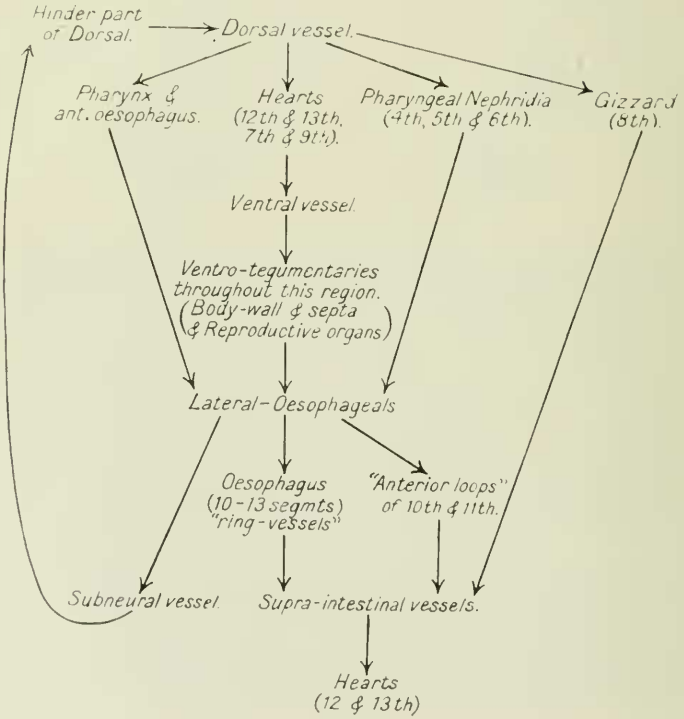
TEXT-FIG. 11.



Semi-diagrammatic representation of 'hearts' in longitudinal sections. A is one of the 'lateral' hearts of the ninth segment with the valves in its lumen and a bulb-like dilatation at its ventral end before it joins the ventral vessel. *d.v.* = dorsal vessel; *ht.* = heart; *v.* = valves; *si.v.* = supra-intestinal vessel.

the region of the body behind the thirteenth segment, is the distributing vessel and supplies blood through the ventro-tegumentaries to the body-wall, the integumentary nephridia as well as the spermathecae and seminal vesicles, the ovaries, and the oviducts. But it does not supply blood to the gut as it does in the hinder region; there are no ventro-intestinals here, and the function of supplying blood to the gut here is taken over partly by the dorsal vessel which supplies blood to the gizzard in the eighth segment and the pharynx and oesophagus in front, and partly by the lateral oesophageals. These vessels

in this region of the body are the counterpart of the subneural, the commissural, and the septo-intestinals of the hinder region, and bring blood from the periphery to the main stream and to the gut. They receive a pair of branches bringing blood from the body-wall, the septa, and other organs of the body, e.g. the nephridia (pharyngeal and integumentary) and the reproduction organs. The part of the oesophagus behind the gizzard is supplied with blood by the lateral oesophageals which lie intimately attached along the ventro-lateral aspect of the oesophagus. The blood from the oesophagus (ten to thirteen) ('ring-vessels') and the gizzard is collected by the supra-intestinal vessel, which also receives blood directly from the lateral oesophageals through the 'anterior loops' of the tenth and eleventh segments, and is conveyed to the hearts in the twelfth and thirteenth segments. The course of blood can be represented as follows :—



6. Summary.

1. The typical arrangement of the blood-system in Pheretima occurs in the region of the body behind the fourteenth segment, the first fourteen segments forming the cephalized region. The main longitudinal trunks are the same as in Lumbricus, except that the lateral neurals are absent as in Allolobophora. The dorsal vessel receives two pairs of dorso-intestinals and one pair of commissurals in each segment behind the cephalized region.

2. The intestinal blood-plexus is both an external and an internal one, and three regions can easily be distinguished. The first is internal, and extends from the fourteenth to the twenty-sixth segment; the second is both external and internal, is co existent with the typhlosole, and extends over the larger part of the gut; and the third is only external, and is confined to the rectal or post-typhlosolar part of the gut (last twenty-three to twenty-six segments).

3. The commissural vessel of Pheretima is a compound vessel, and represents both the 'dorso-sous-nervien' of Lumbricus and the intestino-tegumentary of Megascolex. The capillaries of the integument are not like those of Lumbricus but like those of Moniligaster, and there is a close 'parallelism' between an 'artery' and a 'vein' in the body-wall, in which the two pass into each other through a number of capillary loops.

4. There are four pairs of 'hearts' which connect the dorsal with the ventral vessel, and five pairs which supply blood directly to the various organs in the cephalized region. There are two pairs of non-contractile 'anterior loops' connecting the lateral oesophageals with the supra-intestinals, these loops being the counterpart of the connexions of the lateral oesophageals with the dorsal and the parietal in the tenth and twelfth segments respectively of Lumbricus. The subneural vessel is absent in the first fourteen segments, and is continuous with the lateral oesophageals of the anterior region.

5. As regards the course of circulation of the blood, the chief

fact is that the dorsal vessel is wholly 'venous' behind the 'hearts' and wholly 'arterial' in the region of the 'hearts' and in front (the whole of the cephalized region). The examination of valves and experiments by cutting and pinching the blood-vessels in Pheretima confirm the results of Johnstone for Lumbricus as regards the course of blood in dorso-intestinals and commissurals and make Bourne's theory untenable. The ventral vessel is the arterial trunk throughout, while the venous function of the dorsal and subneural behind is taken up by the lateral oesophageals in the cephalized region. The thin-walled and non-contractile 'loops' of the tenth and eleventh segments must be distinguished from the thick walled and contractile 'hearts' of the other cephalized segments, the 'loops' being the channels for conveying blood from the lateral oesophageals to the supra-intestinals.

List of References.

1. Bourne, A. G.—"On Megascolex coeruleus and a Theory of the Course of the Blood in Earthworms", 'Quart. Journ. Micro. Sci.', vol. 32, 1891.
2. —— "On Moniligaster grandis", ibid., vol. 36, 1894.
3. Beddard, F. E.—"On the Structure of a New Genus of Oligochaeta, and on the Presence of Anal Nephridia in Acanthodrilus", ibid., vol. 31, 1890.
4. —— 'A Monograph of the Oligochaeta'. Oxford, 1895.
5. Benham, W.—"Studies on Earthworms", 'Quart. Journ. Micro. Sci.', vol. 26, 1886.
6. —— "The Nephridium of Lumbricus and its Blood-supply", ibid., vol. 36, 1891.
7. Bahl, K. N.—"On a New Type of Nephridia in Indian Earthworms of the genus Pheretima", 'Quart. Journ. Micro. Sci.', vol. 64, 1919.
8. Harrington, N. R.—"The Calciferous Glands of Earthworms, with an Appendix on Circulation", 'Journ. of Morphology', vol. 5, Supplement, 1899.
9. Jaquet.—"Recherches sur le système vasculaire des Annélides", 'Mitth. Zool. Stat. Neap.', Bd. VI, 1885–6.
10. Johnstone, J. B., and Johnson, Sarah W.—"The Course of Blood-flow in Lumbricus", 'American Naturalist', vol. 36, 1902.
11. Johnstone, J. B.—"On the Blood-vessels, their Valves, and the Course of the Blood in Lumbricus", 'Biological Bulletin', vol. 5, 1903.

12. Lankester, E. Ray.—" The Anatomy of the Earthworm ", ' Quart. Journ. Micro. Sci.', 1865.
13. Perrier.—" Études sur l'organisation des lombriciens terrestres ", ' Arch. Zool. Exp.', t. ix, 1881.
14. Stephenson, J.—" On Intestinal Respiration in Annelids : with Considerations on the Origin and Evolution of the Vascular System in that Group ", ' Trans. Roy. Soc. Edin.', vol. 49, 1914.
15. Vejdovsky, F.—' System und Morphologie der Oligochaeten ', Prag. 1884